Taxonomic reassessment of *Polysiphonia foetidissima* (Rhodomelaceae, Rhodophyta) and similar species, including *P. schneideri*, a newly introduced species in Europe.

PILAR DÍAZ-TAPIA[1], MYUNG SOOK KIM[2], ANTONIO SECILLA[3], IGNACIO BÁRBARA[1] AND JAVIER CREMADES[1]

[1]Coastal Biology Research Group. Facultade de Ciencias, University of A Coruña. Campus da Zapateira s/n. A Coruña, 15071. Spain

[2]Department of Biology and Research Institute for Basic Sciences, Jeju National University, 66 Jejudaehankno, Jeju-si, Jeju-do, 690-756, Korea

[3]Departamento de Biología Vegetal y Ecología, Facultad de Ciencia y Tecnología, University of Basque Country, Apdo. 644. Bilbao 48080, Spain

Correspondence to: Pilar Díaz Tapia. E-mail: pdiaz@udc.es.

Running title: *Polysiphonia foetidissima* and *P. schneideri* in Europe

Abstract

Morphological and molecular studies were carried out on two *Polysiphonia* with 6-9 pericentral cells from the Atlantic Iberian Peninsula. A detailed description is provided for *P. foetidissima,* a poorly known species originally described from the British Isles that is widespread and abundant in the Iberian Peninsula. *Polysiphonia schneideri*, originally described from Atlantic USA and Bermuda, is reported for the first time in Europe (Southern Spain). It was collected attached to man-made structures such as floating docks and artificial substrates for aquaculture and is believed to be a newly introduced species in Europe. In addition, the taxonomy of seven morphologically similar *Polysiphonia* was reassessed. A comparative study of type materials showed that the Mediterranean *P. stuposa* is morphologically different from its alleged synonym *P. foetidissima*. Instead, molecular and morphological evidence showed that *P. foetidissima* is synonym of the widely reported (Atlantic and Pacific) *P. tepida*. *Polysiphonia foetidissima* was also shown to be remarkably different from *P. brodiaei, P. exilis*, *P. isogona* and *P. schneideri*. The phylogenetic relationships of *P. foetidissima* and *P. schneideri* with *Neosiphonia* and *Polysiphonia sensu stricto* are discussed.

Key words: molecular phylogeny, morphology, *Polysiphonia, P. foetidissima, P. exilis, P. isogona*, *P. schneideri, P. stuposa, P. tepida*, taxonomy.

Introduction

The genus *Polysiphonia* Greville is one of the largest genera of Rhodophyta (Womersley, 1979; Mamoozadeh & Freshwater, 2012). Almost 1000 species names have been assigned to this genus at one time or another and, at present, it is thought to contain approximately 200 recognized species (Guiry & Guiry, 2012). This large number of species along with inadequate early descriptions and a paucity of diagnostic features in dried herbarium specimens make the verification of species from different areas a challenge (Womersley, 1979). The problem is further aggravated by the frequency and variety of species, often misidentified, mentioned in most ecological accounts and checklists (Womersley, 1979), and unsupported by herbarium material. On the other hand, new species of *Polysiphonia* continue to be described (Maggs & Hommersand, 1993; Kim & Lee, 1999; Stuercke & Freshwater, 2010; Bárbara *et al.* 2013). Many of these new species had previously remained unnoticed owing to their small size, their confinement to restricted habitats, and the challenges of an identification that requires of the study of morphological details. In some cases, *Polysiphonia* species have remained undescribed due to the absence of consistent diagnostic features to delineate species, and only recently molecular tools have provided objective data to separate them (e.g. Stuercke & Freshwater, 2010). Likewise, some introduced species of *Polysiphonia* closely resemble native species and molecular analyses provide useful tools for detecting and identifying these species in non-native areas (McIvor *et al.*, 2001; Geoffroy *et al.*, 2012). In this regard, numerous introductions of macroalgae to the Atlantic European coasts have been reported over the past four decades (Farnham, 1980; Maggs & Stegenga, 1999; Hewitt *et al.*, 2007; Bárbara *et al.*, 2008; Couceiro et al., 2011; Mineur *et al.*, 2012). Moreover, the actual number of invaders and their impacts may have been seriously underestimated (McIvor *et al.*, 2001). The only *Polysiphonia s. l.* species previously reported as introduced to the Atlantic Europe are *Neosiphonia harveyi* (J.W. Bailey) M.-S.Kim, H.-G.Choi, Guiry et G.W.Saunders and *P. morrowii* Harvey from Atlantic North America and Japan, respectively (Maggs & Stegenga, 1999; McIvor *et al.*, 2001). Nonetheless, the challenging species discrimination noted above suggests that other cases of cryptic introductions might have been overlooked within this difficult group.

Two small species of Polysiphonia with 6-9 pericentral cells were found during our recent general algal collections along the Atlantic Iberian Peninsula. These species proved to be *P. foetidissima* Cocks ex Bornet and *P. schneideri* Stuercke et Freshwater. Here we provide a detailed description of these taxa, and an integrative morphological and molecular taxonomic reassessment of a group of similar species that also includes *P. isogona* Harvey, *P. exilis* Harvey, *P. kappannae* Sreenivasa Rao, *P. nizamuddinii* Farooqui et Begum, *P. stuposa* Zanardini ex Kützing, *P. tepida* Hollenberg, and certain small and creeping forms of *P. brodiei* (Dillwyn) Sprengel.

Materials and methods

Polysiphonia specimens were collected along the Atlantic Iberian Peninsula and Southern France during 2002-2011 (Table S1). *P. foetidissima* was collected at 28 sites along the Atlantic coasts of the Iberian Peninsula, in sand-covered rocks from the intertidal to the subtidal. The material of *P. schneideri* was collected in 2011 at 2 sites from Cádiz, Southern Iberian Peninsula, on fouling aquaculture floating structures and floating docks in a harbour.

Material collected for morphological studies was preserved in 4% Formalin in seawater. Microscope slides were mounted in a mixture of 20% Karo® Syrup (ACH Foods, Memphis, TN, USA) and 80% distilled water. Line drawings were made using a *camera lucida* and photomicrographs were taken with a Olympus C-5060 digital camera mounted on a Olympus BX50 microscope (Tokyo, Japan). Representative specimens were deposited at the herbarium of the University of Santiago de Compostela (SANT) and the herbarium of the University of the Basque Country (BIO). The type materials of *Polysiphonia foetidissima*, *P. tepida*, *P. stuposa* and *P. exilis* were studied at PC or borrowed from MICH, MEL and L, and TCD, respectively. Herbarium abbreviations follow the online *Index Herbariorum* <http://sweetgum.nybg.org/ih/>.

Material collected for molecular analysis was dried in silica gel and total genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following manufacturer's instructions. The extracted DNA was stored at -20 ºC and used to amplify the *rbc*L region with the forward primer rbcLF145 combined with the reverse primer rbcLR898, and the forward primer rbcLF762 combined with the reverse primer rbcLR1442 (Kim *et al.*, 2010). PCR amplification was performed in a total volume of 25 μl containing 0.5 U of *TaKaRa Ex Taq* DNA polymerase (Takara shuzo, shiga, Japan), 2.5 mM of each dNTP, 2.5 μl of the 10X *Ex Taq* Buffer (Mg^{2+} free), 2 mM $MgCl_2$, 10 pmol of each primer, and 1-10 ng of template DNA. PCR was carried out with an initial denaturation at 96 ºC for 4 min, followed by 35 cycles of denaturation at 94 ºC for 1 min, annealing at 50 ºC for 1 min, and extension at 72 ºC for 2 min with a final extension at 72 ºC for 7 min. PCR products were purified using the AccuPrep PCR Purification Kit (Bioneer, Daejeon, Korea) according to the manufacturer's instructions.

Electropherogram outputs from each sample were edited with the program Chromas 1.45 (Technelysium, Queensland, Australia) and *rbc*L sequences were aligned using BioEdit 7.1.3 (Tom Hall, Ibis Biosciences, Carlsbad, USA). Sequences were produced for 17 specimens of *Polysiphonia* and aligned with 30 sequences for other *Polysiphonia* species obtained from GenBank plus two genera (*Lophosiphonia* and *Herposiphonia*) used as the outgroup. The resulting alignment was 1241 bp long and contained 462 variable (37%) and 380 (30%) phylogenetically informative sites. The best-fit nucleotide substitution model for our sequence data was determined with the likelihood ratio test implemented in ModelTest 3.7 (Posada & Crandall, 1998) and found to be a general time reversible (GTR) model with gamma correction for among-site variation (Γ) and proportion of invariable sites (I). To confirm the taxonomic position of the two species of *Polysiphonia*, maximum likelihood (ML) analyses were performed with PAUP 4.0 (Swofford, 2002). ML trees were estimated using a heuristic search with 100 random addition sequence replicates, and TBR branch swapping. ML bootstrap analyses were performed with 1,000 replicates to test node stability.

Results

Phylogenetic analysis of rbcL

Twelve specimens of *Polysiphonia foetidissima* from the Atlantic Iberian Peninsula and Southern France and one of *Polysiphonia tepida* from USA (as *Neosiphonia tepida* (Hollenberg) Guimaraes et Fujii) were nearly identical with minor differences of up to 0.4% divergence. One specimen of *P. schneideri* from the Atlantic Iberian Peninsula was grouped together with specimens from Panama, USA, and Bermuda (UK), with

0.1-0.8% intraspecific divergence. Three *P. brodiei* from Spain and one specimen from Ireland showed 0-0.3% intraspecific divergence.

In the phylogenetic tree (Fig. 1), all specimens of *Polysiphonia foetidissima* formed a monophyletic clade with strong support (99 % for ML). This species was sister to *P. isogona* with 1.7-1.8% interspecific divergence. The ML analysis of *rbc*L data showed that *P. foetidissima* was conspecific with *P. tepida* from North Carolina and both were clearly separated from other species. Monophyly of the other three species from Spain was supported by strong bootstrap values: 100 % for *P. schneideri*, 100 % for *P. elongata*, and 100 % for *P. brodiei*. *P. schneideri* formed a sister group (80% bootstrap support) with a clade including *P. forfex* Harvey, *P. strictissima* J.D. Hooker et Harvey and *N. harveyi* (J.W. Bailey) M.-S. Kim, H.-G. Choi, Guiry & G.W. Saunders. Sequences of *P. elongata* and *P. elongella* Harvey have a 5.8% divergence and their sister relationship is supported by a moderate bootstrap value (82%). The sister relationship of *P. brodiei* and *P. fibrillosa* (Dillwyn) Sprengel from Ireland has 100% bootstrap support and their sequences have a 3.2-3.4% divergence.

Morphological observations

Polysiphonia foetidissima Cocks ex Bornet, 1892: 314.

Synonyms: *Polysiphonia tepida* Hollenberg, 1958; *Neosiphonia tepida* (Hollenberg) S.M. Guimarães et M.T. Fujii in Guimaraes *et al.*, 2004; ? *Polysiphonia kappannae* Sreenivasa Rao, 1967; ? *Polysiphonia nizamuddinii* Farooqui et Begum, 1978.

Lectotype: PC 0146017 (Figs 2-6), Herb. Cock´s “Algarum Fasciculi” no. 29.

Lectotype locality: Mount Edgcumbe, Plymouth, Cornwall, British Isles.

Description of type material

Thalli forming dense tufts 7 cm high consisting of interwoven prostrate and erect axes (Fig. 2), brownish-red in color. Axes ecorticate, with 7-8 pericentral cells (Fig. 3). Prostrate axes 80-110 µm in diameter and segments 2.2-3.8 diameters long; with rhizoids cut off from pericentral cells (Fig. 4). Erect axes 70-120 µm in diameter, with segments 1.7-3.3 diameters long. Branches formed in the axils of trichoblasts at the apex of erect axes (Fig. 5), mostly at intervals of 6-8 segments, alternate. Trichoblasts abundant; borne 3-4 segments apart in a 1/4 spiral divergence, deciduous and leaving conspicuous scar cells (Fig. 6).

Tetrasporangia in spiral series in upper parts of erect axes, one per segment.

Description of material from Iberian Peninsula

Vegetative morphology

Thalli forming dense turfs up to 2 cm high, covering up to 30 cm, and developing a large horizontal system of interwoven decumbent axes growing from erect apices (Fig. 7). Erect axes quickly becoming creeping by means of the development of rhizoids in basal segments (Fig. 8). The erect axes are alternately branched up to 5 orders, bearing short branches (Figs 8-10). Thallus are brownish-red in color and erect axes having soft and flaccid texture.

Axes ecorticate, with (6-) 7-8 (-9) pericentral cells (Figs 13-17). Creeping axes (60-) 90-150 (-180) µm in diameter, with segments (0.4-) 0.6-1.1 (-1.6) diameters-long and with conspicuous scar cells of trichoblasts which often give rise to adventitious branches (Fig. 12). Rhizoids cut off from the posterior end of pericentral cells; typically, only one rhizoid per segment, often with digitate pads when totally developed (Fig. 12); 30-60 (-80) µm in diameter and up to 800 (-1600) µm long. Erect axes growing from apical cells 10-12.5 µm in diameter, major axes reaching (50-) 60-110 (-130) µm in diameter; segments (0.4-) 0.5-0.9 (-1.1) diameter long. Exogenous branches formed at the tips of erect axes in the axils of trichoblasts (Figs 9, 11), mostly at regular intervals of 6-8 (-9) segments, alternate (Figs 9-11). Trichoblasts usually numerous, but sometimes scarcely developed; borne (2-) 3-4 (-5) segments apart in a 1/4 spiral divergence, 12.5-17.5 µm in diameter at the base, pseudodichotomously branched up to 3 times, deciduous and leaving conspicuous scar cells (Fig. 9). The branching pattern varies along the axes: branches arising exogenously from apices of erect axes every 6-8 segments; later, the basal parts of erect axes develop rhizoids and become creeping; and then adventitious branches develop from some scar cells of these basal parts,. Short prostrate axes with a prominent apical cell and without trichoblasts arising from adventitious branches.

Reproductive morphology

Tetrasporangia one per segment, forming long series in a slight and irregular spiral, with up to 8 (-12) mature tetrasporangia. Series are frequently interrupted by segments lacking or with aborted tetrasporangia, then tetrasporangia often appearing scattered or forming short linear series of up to 4 (-6) mature ones. Tetrasporangia are ovate, (35-) 40-60 (-65) µm in diameter (Figs 18, 19).

Gametophytes dioecious. Procarps consist of a four-celled carpogonial branch and two sterile cells borne on the supporting cell (Fig. 20). Cystocarps globular to ovoid when mature (Figs 21, 22), (220-) 300-350 µm high and (160-) 210-285 (-300) µm in diameter, with an ostiole (75-) 100-150 (-170) µm in diameter. Carposporangia clavate, (53-) 60-80 (-90) µm long and (18-) 20-25 (-30) µm wide.

Spermatangial axes located at the apical parts of erect main axes and branches (Figs 23, 24), borne 3-4 segments apart; developed on the first trichoblast furcation, the other branch of which persisting at maturity (Fig. 23). Spermatangial axes cylindrical (Fig. 23), sometimes furcated (Fig. 25), (100-) 110-170 (-188) µm long and (30-) 35-40 (-45) µm in diameter, with 1-3 sterile terminal cells when mature (Fig. 25). They consist of a central axis with four pericentral cells arising per axial cell; pericentral cells bear a layer of quadrangular to elongate spermatangial mother cells of 12.5 × 10-12.5 µm, that develop elongate spermatia 10-12.5 × 5 µm.

Polysiphonia foetidissima was collected throughout the year. Tetrasporangial thalli were frequently found year-round and they were abundantly observed in half of the collected samples. In comparison, gametophytes were more rarely observed. Male and female structures were detected in less than 20% of the collections and only in April-June and September-October.

Habitat and distribution

In the Iberian Peninsula, *Polysiphonia foetidissima* grows at moderately to extremely wave-exposed sites, usually on sand-covered rocks from the middle to the lower intertidal. It develops dense turfs over bare rock but it also grows over other turf-forming seaweeds like *Rhodothamniella floridula* (Dillwyn) Feldmann, *P. nigra* (Hudson) Batters, *Ophidocladus simpliciusculus* (P.L. Crouan et H.M. Crouan) Falkenberg or *Pterosiphonia pennata* (C. Agardh) Sauvageau. Interestingly, *P.*

foetidissima was occasionally found on subtidal maërl in a single collection from a maërl bed (10 m depth) in Ría de Arousa (Galicia).

Polysiphonia foetidissima was found in 28 locations throughout the Atlantic Iberian Peninsula (Fig. 26). Moreover, our examination of herbarium material from other regions confirms its occurrence at Stackpole Quay, Wales (materials collected and identified by F. Bunker and C. Maggs in 1998); Atlantic France (Sant Vaast la Hogue: L 0796156; Biarritz: L 796154, L 796155, SANT-Algae 25433), and Atlantic North America (Bermuda: L 796144, MICH Phycotheca Boreali Americana, Algae of Bermuda Nº 1890; Texas: MICH Port Mansfield, South Padre Island, 10.viii.1993). In addition, both molecular data and morphology support the conclusion that collections from Florida (USA) identified as *N. tepida* are conspecific with *P. foetidissima*.

Polysiphonia schneideri Stuercke *et* Freshwater, 2010: 302.

Holotype: MICH (WNC-8782).

Type locality: Wrightsville Beach, New Hanover County, North Carolina, USA.

Vegetative morphology

Thallus predominantly erect (Fig. 27), up to 5 cm long, attached to the substratum by rhizoids that grow from short, decumbent basal parts. Plants red to purple in colour. Rhizoids cut off from pericentral cells (Fig. 28), growing abundantly in basal parts of axes, often two per segment. Axes with 6-7 pericentral cells (Figs 29, 30), ecorticate and (100-) 150-300 (-350) µm in diameter. Erect axes pseudodichotomously or irregularly branched, up to 7 orders; branches formed in the axils of trichoblasts (Fig. 31). Trichoblasts scarce, growing several segments apart, irregularly arranged (Fig. 32).

Reproductive morphology

Tetrasporangia spherical, (75-) 80-100 µm in diameter, formed at the apical parts of erect axes in straight series, distending branches when mature (Fig. 33). Gametophytes are dioecious. Procarps consist of a four-celled carpogonial branch and two sterile cells borne on the supporting cell (Fig. 34). Cystocarps globular to ovoid when mature (Fig. 35), 350-450 (-500) µm high and (270-) 300-460 (-500) µm in diameter, with a narrow ostiole. Carposporangia clavate, (75-) 85-110 (-125) µm long and (30-) 35-45 (-50) µm wide. Spermatangial branches borne several segments apart in upper parts of erect axes and developed on the first trichoblast furcation, the other branch of which persisting at maturity. Spermatangial branches are cylindrical to conical, (125-) 150-200 (-240) µm long and (25-) 35-45 (-60) µm in diameter, with several apical sterile cells (Fig. 36). *P. schneideri* was collected in February and June, when tetrasporophytes, male and female gametophytes were found.

Habitat and distribution.

Polysiphonia schneideri was found as a fouling organism at two sites in southern Spain (Fig. 26). One site consisted of aquaculture structures placed in the intertidal of the Bay of Cádiz where it was found entangled with *P. denudata* (Dillwyn) Greville ex Harvey. The other site consisted of floating structures in the harbour of Barbate where *P. schneideri* was growing on *Balanus* sp. and ascidians, together with *Neosiphonia harveyii*, *Antithamnionella ternifolia* (J.D. Hooker et Harvey) Lyle and *Antithamnion cruciatum* (C. Agardh) Nägeli.

Discussion

The material of *Polysiphonia foetidissima* from the Atlantic Iberian Peninsula shares all the main taxonomic features with the type material. This red alga is a poorly known species first described from specimens collected in the British Isles (Bornet, 1892) but that has been reported for a small number of locations at mid-low latitudes on both sides of the North Atlantic Ocean (see Fig. 37 and references therein). *P. foetidissima* shows some distinctive morphological features rarely found in other *Polysiphonia*, namely: trichoblasts 3-4 segments apart, and spermatangial branches sometimes furcated. Maggs & Hommersand (1993), after examination of the type material, reported that trichoblasts were apparently borne on every segment. However, our own observations of the same type material indicate that trichoblasts are actually separated by the 3-4 naked segments noted above. Falkenberg (1901) and Hollenberg (1942) considered that the position of trichoblasts is a diagnostic feature in *Polysiphonia*. Usually, a single segment intervenes between successive trichoblasts. However, a few species are characterized by the occurrence of two or more segments between successive trichoblasts, the same feature that we have observed in *P. foetidissima*. Interestingly, several authors have noted that when trichoblasts are separated by naked segments, the tetrasporangia develop in straight series (Hommersand, 1963; Kapraun, 1977; Kim *et al.*, 2000; Stuercke & Freshwater, 2008). However, this alleged correlation between traits does not apply to *P. foetidissima* because its tetrasporangia are arranged in spiral series.

Based on the descriptions provided in the literature, *Polysiphonia foetidissima* is closely similar to *P. stuposa*, *P. tepida*, *P. kappannae, P. nizamuddinii* and *P. isogona*. Furthermore, *P. exilis*, *P. confusa* Hollenberg, *P. schneideri* and certain small, creeping forms of *P. brodiei* are also remarkably similar. By comparison, the 15 other species of

Polysiphonia reported worldwide with a number of pericentral cells similar to that in *P. foetidissima* are distinguished from the latter in at least one or more of the following diagnostic features: rhizoid anatomy (in open connection *vs.* cut off from pericentral cells), branch development (not associated with trichoblasts *vs.* in the axils of trichoblasts), and/or habit (erect *vs.* prostrate or decumbent). These are some of the features commonly used to discriminate the various species of *Polysiphonia* (Falkenberg, 1901; Hollenberg, 1942; Segi, 1951; Meñez, 1964; Kapraun, 1977; Womersley, 1979; Maggs & Hommersand, 1993; Kim & Lee, 1999; Stuercke & Freshwater, 2008).

Polysiphonia stuposa is another poorly known species. Originally described for Dalmatia (Kützing, 1864), this red alga is thought to be restricted to the Mediterranean (Fig. 37 and references therein). Its separation from *P. foetidissima* has been questioned by some authors. Hauck (1885) regarded *P. foetidissima* (name in Cocks' exsiccate not yet validly published) as synonymous with *P. stuposa* but the name was subsequently validated by Bornet (1892). However, various latter authors still followed Hauck's criterion and erroneously reported *P. stuposa* as synonymous with *P. foetidissima* (De Toni, 1903; Batten, 1923; Newton, 1931; Ardré, 1970). Maggs and Hommersand (1993) did not reach a definitive conclusion either, noting that the type material of these two species appeared to be very similar. However, they still followed the criterion of Bornet and retained the name *P. foetidissima* for the collection from the British Isles but pointing out that the name *P. stuposa* predates the probably conspecific *P. foetidissima*. More recently, Gómez-Garreta *et al.* (2001) considered *P. foetidissima* as synonym of *P. stuposa* under which name grouped all the records for these two species along the Mediterranean (Fig. 37).

According to the literature, the only distinctive characters previously known for *P. stuposa* were the 6-8 pericentral cells, the absence of trichoblasts, and the occurrence of segments 1-2 diameters long (Kützing, 1864). The absence of trichoblasts distinguishes this species from *P. foetidissima*, although several authors have argued that the abundance of trichoblasts is variable in several species of *Polysiphonia* (Hollenberg, 1942, 1968; Guimarães *et al.*, 2004; Stuercke & Freshwater, 2008). Our detailed study of the type material of *P. stuposa* (Figs 38-40) (Holotype: MEL 2324435; Isotypes: L 0056079, 0056078) and other collections from the Adriatic (L796145, 796147-796153, 796158) reveals that it can indeed be unambiguously distinguished from *P. foetidissima,* the main distinctive feature being the origin of branches, which are not associated with trichoblasts in the case of *P. stuposa* (Fig. 40). This observation prevents us from considering these two species as taxonomic synonyms and suggests that the range of *P. stuposa* as well as the occurrence of *P. foetidissima* within the Mediterranean requires further investigation.

Polysiphonia tepida, reported from temperate coasts worldwide (Fig. 37 and references therein), was first described for North Carolina (Hollenberg, 1958). Its relationship with *P. foetidissima* has been rarely studied despite the fact that these two species seemingly have overlapping ranges along the Atlantic coast of North and Central America (Fig. 37). Hollenberg (1958) distinguished *P. tepida* from *P. foetidissima* because the latter (Bermuda material) had branches not arising in connection with trichoblasts. He also noted that the cortication at the base of some specimens of *P. foetidissima* from the British Isles reported by Newton (1931) differed from what he observed in *P. tepida*. Afterwards, only Taylor (1960) reported both *P. foetidissima* and *P. tepida* in the same work, but it seems he largely followed the criterion originally proposed by Hollenberg (1958). Unfortunately, Hollenberg did not study the type material of *P. foetidissima* that, according to our observations as well as those provided by Maggs & Hommersand (1993), has branches formed in the axils of trichoblasts and is ecorticate throughout. These features are also found in the holotype of *P. tepida* (MICH, Herbarium of W.R. Taylor, collected by H.L. Blomquist in 1940 in Beaufort, North Carolina, USA; Figs 43-47) which is characterized by a predominantly prostrate habit (Fig. 43), axes with 7-8 pericentral cells (Fig. 44), rhizoids cut off from pericentral cells (Fig. 45), and abundant trichoblasts separated by 3-4 naked segments (Fig. 47; for a more detailed comparative analysis see Table 1). The similarity between *P. foetidissima* and *P. tepida* is likewise consistent with our *rbc*L data since the sequence produced by Mamoozadeh & Freshwater (2011) for *P. tepida* from Florida (as *Neosiphonia tepida*) showed a very small divergence (<0.4%) with our 12 collections of *P. foetidissima* from the Atlantic Iberian Peninsula. Therefore, we are compelled to propose the taxonomic synonymy of these two species, with *P. foetidissima* having nomenclatural priority.

The recent transfer of *Polysiphonia tepida* to *Neosiphonia* (Guimarães *et al.*, 2004) is questioned here. This transfer may possibly be based on misidentified material from Brazil because it is reported to show traits (trichoblasts on every segment, see Oliveira Filho 1969: pl XXIII, Fig. 136, Guimarães *et al.*, 2004) that do not match either our observations of the type material of *P. tepida* or the descriptions provided by other authors for collections from Atlantic North America (Hollenberg, 1958; Kapraun, 1977; Schneider & Searles, 1991: Fig. 558; Dawes & Mathieson, 2008; Mamoozadeh & Freshwater, 2011). A similar confusion may also explain some recent reports of *P. tepida* in the Canary Islands (Rojas-González & Afonso-Carrillo, 2008). Instead, the morphological features of these plants from Brazil and the Canary Islands suggest that they could belong to a new species of *Neosiphonia*. That, surely, warrants further research.

Polysiphonia kappannae and *P. nizamuddinii* were described from India (Sreenivasa Rao, 1967) and Pakistan (Farooqui & Begum, 1978), respectively (Fig. 37), but no additional reports have been provided after their original descriptions. They are very similar to one another as well as to *P. foetidissima* (Sreenivasa Rao, 1967; Kapraun, 1977). Moreover, the detailed descriptions provided by Sreenivasa Rao (1967) and Farooqui & Begum (1978) indicate that these two red algae can only be distinguished from *P. foetidissima* in the linear arrangement of tetrasporangia. However, tetrasporangia in *P. foetidissima* are arranged in slight and irregular spiral series and sometimes appear forming short straight series. Thus, considering the agreement in other features, we are tempted to speculate that they might actually be taxonomic synonyms with *P. foetidissima*. Despite our efforts, we did not have the opportunity to examine the type collections of any of these species.

Polysiphonia exilis, originally described by Harvey (1853) from Key West (Florida) and subsequently recorded from other locations (Table 1), shares several diagnostic features with *P. foetidissima* (Table 1). However, their conspecificity seems unlikely according to our observations. We have examined the type material of *P. exilis* (TCD0012730, Figs 48-55) finding that the number of pericentral cells (9, see Fig. 50) is larger than what is usually observed in *P. foetidissima*. Likewise, the occurrence of trichoblasts on every segment (Figs 52, 53) and the irregular branching pattern that often results in secund series (Fig. 49) are other features clearly different from what is observed in *P. foetidissima*. Moreover, branches in *P. exilis* might not form at the apexes since we did not observe any branches close to the tips. Conversely, we found numerous cicatrigenous branches along the erect axes (Figs 53, 54). In comparison, *P. foetidissima* has exogenous branches and while it also shows cicatrigenous branches, the latter are restricted to prostrate axes or to the basal parts of the erect ones. Finally, and although not observed in the type material, spermatangial axes of *P. exilis* lack sterile apical cells (Kapraun & Norris, 1982; Abbott, 1999).

Polysiphonia confusa, also, is morphologically similar to *P. foetidissima* (see Table 1). This *Polysiphonia* was originally described from California (Hollenberg, 1961) and its distribution range seems restricted to the Pacific coasts of America. Again, the main distinctive trait from *P. foetidissima* is the occurrence of trichoblasts on every segment in *P. confusa*. Yet, other distinctive features are: 1) a lower number of pericentral cells in *P. foetidissima* (7-8 *vs.* 8-10 in *P. confusa*), and 2) branches arising 6-8 segments apart in *P. foetidissima* (at irregular intervals in *P. confusa*, see Hollenberg, 1961; Abbott & Hollenberg, 1976; Hollenberg & Norris, 1977).

Our *rbc*L phylogeny indicates that *Polysiphonia isogona* and *P. foetidissima* are close in evolutionary terms and they could even be regarded as sister species. Actually, the sequence divergence found in this study (1.8%) falls at the upper end of the values reported for intraspecific *rbc*L variability for other *Polysiphonia* (Mamoozadeh & Freshwater, 2011). However, it seems unlikely that these two entities should be regarded as conspecific. Our results indicate intraspecific divergence could be very small within *P. foetidissima*. Variation between our 12 collections from the Iberian Peninsula and a sequence produced for material collected in Florida (as *N. tepida*; Mamoozadeh & Freshwater, 2011) is clearly lower (< 0.4%) that the separation found between *P. foetidissima* and *P. isogona.* Their separation is consistent with differences in some morphological traits since *P. isogona* shows (8-) 9-10 (-12) pericentral cells and wider axes (250-300 µm in diameter) (Adams, 1991; Womersley, 2003). Furthermore, according to Adams (1991), *P. isogona* has trichoblasts borne on every segment (but see Womersley, 2003 for a different interpretation of their arrangement).

Polysiphonia schneideri was recently described from Atlantic North America and Bermuda (Stuercke & Freshwater, 2010). It differs from *P. foetidissima* mostly in its 6-7 pericentral cells, its predominantly erect habit, and its tetrasporangia arranged in straight series (Stuercke & Freshwater, 2010). This is the first record of *P. schneideri* in Europe, and also the first report outside of North America. The identity of the European collections is supported by our molecular data since the divergence estimated for samples collected on both sides of the Atlantic (0.1-0.8%) falls within the range of the values typically reported for intraspecific variation. Moreover, this variation compares well with values reported for collections of *P. schneideri* from western Atlantic (0.41-0.66%) by Stuercke & Freshwater (2010). Our molecular results are consistent with a morphology that fits well the original description of this plant. However, the number of pericentral cells in our collections seems to tend towards seven while in the western Atlantic six pericentral cells are most commonly reported. *Polysiphonia schneideri* was collected in two sites of Cádiz (Andalusia, Southern Spain, Fig. 5) always linked to man-made structures: floating docks and artificial substrates for aquaculture (mostly *Crassostrea gigas* (Thunberg 1793) or *Ruditapes decussatus* (Linnaeus 1758), but also several species of fishes). Man-made structures are commonly considered typical habitats for algal invaders (McIvor *et al.*, 2001) and since it seems absent from pristine sites, *P. schneideri* is believed to be a new introduction to Europe. The occurrence of this species in Cádiz could result from importation of mollusks or from ship fouling which are the commonly reported vectors of seaweeds introductions (Mineur et al., 2007a, b). However, *Polysiphonia* includes a large number of species that are variable in morphology and members of this cosmopolitan genus, including native and non-native species, have often been cryptic, (McIvor *et al.*, 2001; Stuercke & Freshwater, 2010; Geoffroy *et al.*, 2012). Thus, it is difficult to state if *P. schneideri* is a new addition to the European exotic flora or if it is a native overlooked species. It is worth noting that, even in the western Atlantic, *P. schneideri* is also commonly found on artificial substrates (Stuercke & Freshwater, 2010, Mamoozadeh & Freshwater 2012).

Typically, *Polysiphonia brodiei* is erect and heavily corticated (Maggs & Hommersand, 1993). However, this species is extremely variable across habitats and seasons. In this regard, certain small, creeping forms of *P. brodiei* that are slightly corticated to ecorticate (Fig. 56) can be misidentified with *P. foetidissima* (Table 1). Despite their distinctive habit, our molecular results corroborate the conspecificity of the small, creeping forms with other collections of *P. brodiei* (Fig. 1). They can be distinguished from *P. foetidissima* by the presence of trichoblasts and scar cells on every segment in *P. brodiei* (Fig. 58). As a result, *P. brodiei* has spermatangial branches in all segments (Fig. 57) whereas *P. foetidissima* has spermatangial branches 3-4 segments apart. Additional features of *P. brodiei* useful to distinguish it from *P. foetidissima* are the absence of sterile apical cells in the spermatangial branches (Fig. 57) and branches arising from the erect axes 3-4 segments (or trichoblasts) apart in *P. brodiei* (Figs 59-61). We have found that these small, creeping forms usually grow on *Codium adhaerens* C. Agardh along the Iberian Peninsula Atlantic coast. Interestingly, Batten (1923) and Newton (1931) noted that material from the British Isles labeled as *P. foetidissima* sometimes showed cortication at the base. This feature matches our observations for creeping forms of *P. brodiei* and, since part of the material studied by Batten (1923) had been collected on *Codium adhaerens*, they could represent misidentified collections of *P. brodiei*. Unfortunately, their exact identity cannot be confirmed because these reports do not appear to be supported by voucher specimens (Maggs & Hommersand, 1993).

As above mentioned, *Polysiphonia,* with approximately 200 species, is one of the largest genera within Rhodophyta (Mamoozadeh & Freshwater, 2012; Guiry & Guiry, 2012). Recently, *Neosiphonia* was segregated from *Polysiphonia* and 30 species have been transferred to the new genus (Kim & Lee, 1999; Guiry & Guiry, 2012). Moreover, *Polysiphonia* was redefined based on a molecular and morphological study of the type species of the genus and only c. 18 species are currently included in *Polysiphonia s. s.* (Kim & Lee, 1999; Kim *et al.*, 2000; Choi *et al.*, 2001; Kim & Yang, 2005; Mamoozadeh & Freshwater, 2011). The other species previously assigned to *Polysiphonia* are currently regarded as *Polysiphonia s. l.* and our *rbc*L phylogeny supports (100% ML) the monophyly of this group. The rbcL divergence between *P. foetidissima* and other morphologically similar *Polysiphonia* is large enough to support the designation of the former as a distinct taxonomic entity. Also, both our molecular analysis and morphological data indicate that *P. foetidissima* is neither a *Polysiphonia s. s.* nor a *Neosiphonia.* Instead, this species must be considered a member of *Polysiphonia s. l.*. Our *rbc*L phylogeny also places *P. schneideri* as a sister group to *Neosiphonia.* This arrangement fits well our morphological observations since *P. schneideri* has 4-celled carpogonial branches while *Neosiphonia* is characterized by 3-celled ones (Kim & Lee, 1999).

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Table 1. Main taxonomic features of *Polysiphonia foetidissima* and similar species with 6-11 pericentral cells, rhizoids cut off from pericentral cells and prostrate or creeping habit.

	P. foetidissima	*P. schneideri*	*P. brodiei*	*P. confusa*	*P. exilis*	*P. isogona*	*P. kappannae*	*P. nizamuddinii*	*P. stuposa*	*P. tepida*
Type locality	Plymouth, Cornwall UK	Wrightsville Beach, North Carolina, USA	Bantry Bay,Cork, UK	California, USA	Key West, Florida	Blind Bay, New Zealand	Okga Port, India	Paradisepoint, Pakistan	Dalmatia, Croatia	Beaufort, North Carolina USA
Distribution	Atlantic Europe and North America	Western Atlantic, Southern Spain	North Atlantic, Mediterranean, Pacific North America, Australia, New Zealand	Pacific America	Bermuda Caribbean Brazil, Australia Pacific islands, Maldivas	New Zealand, Southern Australia	India	Pakistan	Mediterranean Sea	Atlantic North America
Pericentral cells	(6-) 7-8 (-9)	(5-) 6 (-7)	(6-) 7-8	8-10	8-11	(7-) 9-10 (-12)	7-9	(8-) 9 (-10)	7-8	(6-) 7-8

Cortication	Ecorticate	Ecorticate	Slight to heavy	Ecorticate	Ecorticate	Ecorticate	Ecorticate	Ecorticate	Ecorticate	Ecorticate
Branch origin	Axil of trichoblast	Axil of trichoblast	Axil of trichoblast	Axil of trichoblast	Not associated with trichoblast	Axil of trichoblast	Axil of trichoblast	Axil of trichoblast	Not associated with trichoblast	Axil of trichoblast
Trichoblasts (Abundance; segments between successive; divergence)	Abundant; 3-5; 1/4	Few; not one per segment; irregular	Abundant; one per segment; 1/7-1/8	Abundant; one per segment; 1/4	Abundant; one per segment; 1/4	Variable	Abundant; several; 1/4	Abundant; 3-4; -	Absent	Abundant to scarce; 3-5; 1/4
Carpogonial branch cells; Cystocarp	4; globose	-; globose	4; globose	-	-	-; subsphaerical	-; sphaerical	-; globose	-	-; ovate to urceolate
Spermatangial branches	Basal branch of trichoblasts,	Basal branch of trichoblasts	Basal branch of trichoblasts	-	Basal branch of trichoblasts or	Basal branch of	-	Basal branch of trichoblasts	-	Basal branch of

	sometimes furcated				replacing them	trichoblasts				trichoblasts, sometimes furcated
Tetrasporangia	Spiral series	Linear series	Spiral series	Spiral series	Spiral series	Spiral series	Linear series	Linear series	-	Spiral series
References	This work.	Stuercke & Freshwater (2010), this work.	Maggs & Hommersand (1993), this work.	Hollenberg (1944 as *P. incospicua* Hollenberg nom. illeg.; 1961).	Harvey (1853), Hollenberg (1968), Kapraun & Norris (1982), Schneider & Searles (1997), Abbott (1999), this work.	Adams (1991), Womersley (2003).	Sreenivasa Rao (1967).	Farooqui & Begum (1978).	Kützing (1864), this work.	Hollenberg (1958), Kapraun (1977), this work.

Figure Legends

Fig. 1. Maximum likelihood tree for *Polysiphonia* and their relatives from the plastid-encoded *rbc*L sequence data. The bootstrap values shown above the branches are from 1,000 bootstrap resamplings with Maximum likelihood method.

Figs 2-6. *Polysiphonia foetidissima*: type material. **2.** Holotype (PC 0146017). **3.** Cross section of an axis with 8 pericentral cells. **4.** Rhizoids cut off from pericentral cells (arrow). **5.** Apex showing a branch formed in the axil of a trichoblast (arrow) and trichoblasts or scar cells several segments apart (arrowheads). **6.** Axes with a scar cell of a trichoblast (arrowhead). Scale bars = 1.5 cm (Fig. 2), 25 µm (Figs 3-5) and 90 µm (Fig. 6).

Figs 7-17. *Polysiphonia foetidissima*: vegetative morphology of Iberian specimens. **7.** Entangled decumbent axes on a turf of *Rhodothamniella floridula*. **8.** Habit of vegetative thallus. **9-11.** Erect axes with trichoblasts 3-4 segments apart and branches 7-8 segments apart. **12.** Creeping axis with rhizoids cut off from pericentral cells and two adventitious branches. **13-17.** Cross section of axes with 6-9 pericentral cells. Scale bars = 1 cm (Fig. 7), 1 mm (Fig. 8), 100 µm (Figs 9, 12), 400 µm (Fig. 10), 60 µm (Fig. 11) and 50 µm (Figs 13-17).

Figs 18-25. *Polysiphonia foetidissima*: reproductive morphology of Iberian specimens. **18, 19.** Branches with tetrasporangia in spiral series. **20.** Mature procarp showing the axial cell (ax), the supporting cell (su), one-celled second sterile group (st2) and four-celled carpogonial branch (1-4). **21, 22.** Erect axes with cystocarps. **23, 24.** Apical portions of erect axes with cylindrical spermatangial branches. **25.** Furcated spermatangial branch. Scale bars = 100 µm (Figs 18, 21, 23), 400 µm (Figs 19, 22, 24), 10 µm (Fig. 20) and 50 µm (Fig. 25).

Fig. 26. Distribution of *Polysiphonia foetidissima* (circles) and *P. schneideri* (squares) along the Atlantic Iberian Peninsula.

Figs 27-36. *Polysiphonia schneideri*: vegetative and reproductive morphology of Iberian specimens. **27.** Habit of vegetative thallus. **28.** Rhizoids cut off from pericentral cells (arrow). **29, 30.** Cross sections of axes with 6-7 pericentral cells. **31.** Branches growing in the axils of trichoblasts (arrow). **32.** Trichoblasts borne several segments apart (arrowheads). **33.** Tetrasporangia in straight series. **34.** Procarp with four-celled carpogonial branche (1-4). **35.** Mature cystocarp. **36.** Spermatangial branch formed in a furcation of a trichoblast. Scale bars = 0.5 cm (Fig. 27), 100 µm (Fig. 28), 50 µm (Figs 29-32, 36), 200 µm (Figs 33, 35) and 25 µm (Fig. 34).

Fig. 37. World distribution map of *Polysiphonia foetidissima* and related species. *P. foetidissima* (● type locality, ● reports with descriptions, ○ reports), *P.isogona* (▬ type locality, ▬ reports with descriptions), *P. kappannae* (♦ type locality), *P. nizamudinii* (▼ type locality), *P. schneideri* (* type locality), *Polysiphonia stuposa* (■ type locality, □ reports) and *Polysiphonia tepida* (▲ type locality, ▲ reports with descriptions, Δ reports). References: 1, Kützing (1864); 2, Bornet (1892); 3, Collins & Hervey (1917); 4, Howe (1918); 5, Batten (1923); 6, Newton (1931); 7, Hollenberg (1958); 8, Lancelot (1966); 9, Sreenivasa Rao (1967); 10, Oliveira Filho (1969); 11, Hollenberg (1968); 12,

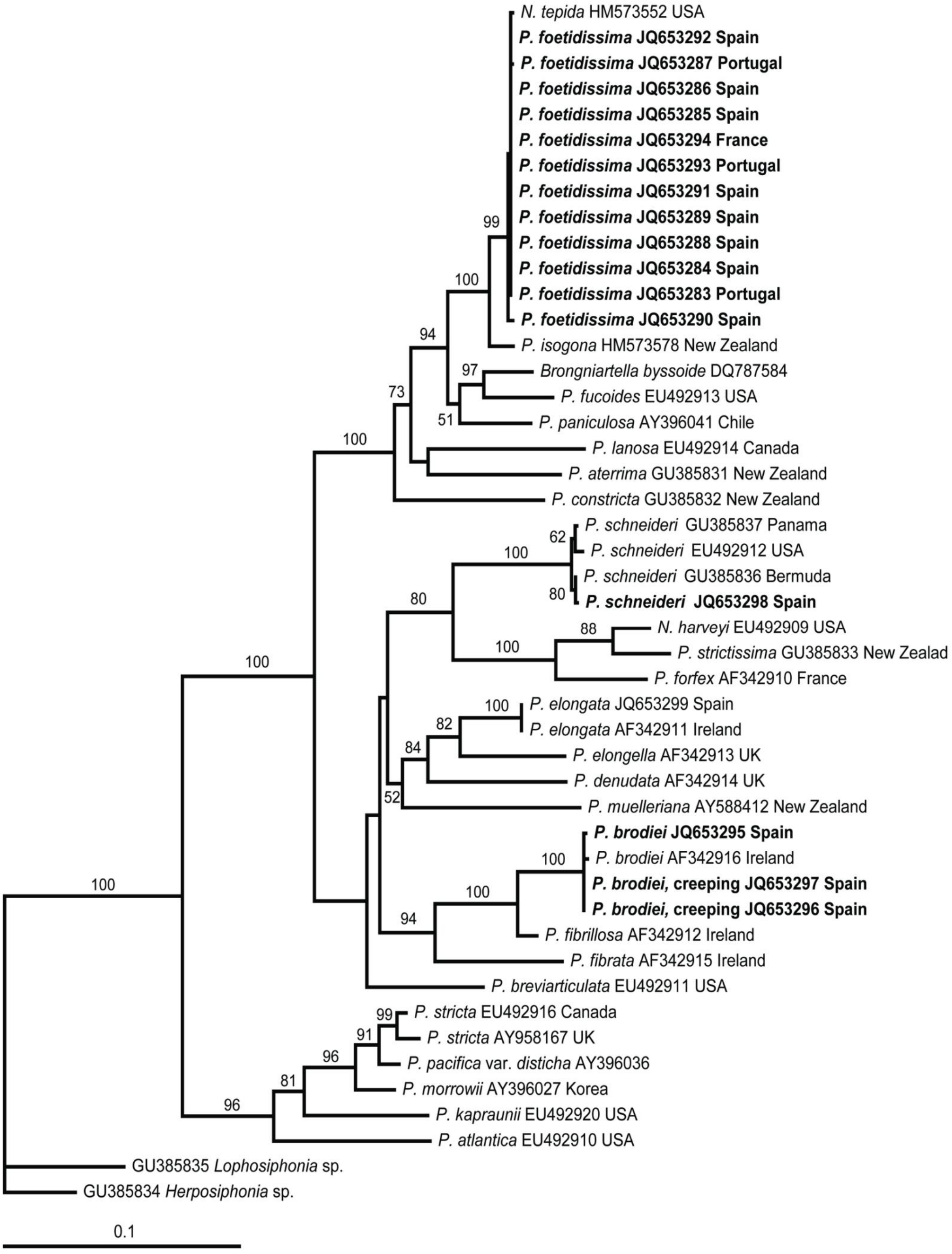
Giaccone (1970); 13, Ardré (1970); 14, Cordeiro-Marino (1977); 15, Kapraun (1977); 16, Farooqui & Begum (1978); 17, Giaccone (1978); 18, Kapraun (1979); 19, Taylor (1960); 20, Schnetter & Schnetter (1981); 21, Weisscher (1983); 22, Audiffred & Prud´homme van Reine (1985); 23, Giaccone *et al.* (1986); 24, Conde & Soto (1986); 25, Silva *et al.* (1987); 26, Ballesteros (1990); 27, Adams (1991); 28, Schneider & Searles (1991); 29, Ballesteros (1993); 30, Lawson *et al.* (1995); 31, Silva *et al.* (1996); 32, Abbott (1999); 33, Coll & Oliveira (1999); 34, Rojas-González & Afonso-Carrillo (2000, 2008); 35, McDermid *et al.* (2002); 36, Womersley (2003); 37, Guimarães *et al.* (2004); 38, Suárez (2005); 39, Duncan & Lee Lum (2006); 40, Tsuda *et al.* (2006); 41, Dawes & Mathieson (2008); 42, Taskin *et al.* (2008); 43, Stuercke & Freshwater (2010); 44 Mamoozadeh & Freshwater (2011).

Figs 38-42. *Polysiphonia stuposa*: type material. **38.** Lectotype (MEL 2324435, collected by Sandri in Dalmatia, Croatia). **39.** Prostrate axis with rhizoids cut off from pericentral cells. **40.** Apex of an erect axis showing branch origin not associated with trichoblasts. **41.** Cross section of an axis with 7 pericentral cells. **42.** Erect axes. Scale bars = 1 cm (Fig. 38), 150 µm (Fig. 39), 30 µm (Fig. 40), 20 µm (Fig. 41) and 600 µm (Fig. 42).

Figs 43-47. *Polysiphonia tepida*: type material. **43.** Holotype (MICH, Herbarium of W.R. Taylor, collected by H.L. Blomquist in 1940 in Beaufort, North Carolina, USA). **44.** Cross section of an axis with 8 pericentral cells. **45.** Creeping axis with a rhizoid cut off from a pericentral cell. **46.** Apical portions of an erect axis with abundant trichoblasts borne 3-4 segments apart and branches arising from the axils of trichoblasts. **47.** Scar cell of a trichoblast on an erect axis. Scale bars = 2 cm (Fig. 43) and 50 µm (Figs 44-47).

Figs 48-55. *Polysiphonia exilis*: type material. **48.** Holotype (TCD 0012730, collected by Harvey at Key West, Florida). **49.** Erect axes with secund branches. **50.** Cross section of thallus with 9 pericentral cells. **51.** Rhizoid cut off from a pericentral cell. **52.** Detail of an erect axis with scar cells of trichoblasts on every segment (arrows) and pericentral cells in straight rows. **53.** Detail of an erect axis with young cicatrigenous branches growing from scar cells (arrowheads); the arrow shows a scar cell of a trichoblast. **54.** Detail of an axis bearing a branch with young tetrasporangia forming a spiral series; the arrowhead indicates a young cicatrigenous branch. **55.** Detail of a prostrate axis bearing erect axes at irregular intervals. Scale bars = 2.5 cm (Fig. 48), 3 mm (Fig. 49), 50 µm (Figs 50-53), 250 µm (Fig. 54) and 650 µm (Fig. 55).

Figs 56-61. *Polysiphonia brodiei*: small and creeping forms in the Iberian Peninsula. **56.** Habit of a tetrasporophyte growing on *Codium adhaerens*. **57.** Spermatangial branches borne on every segment and without sterile apical cells. **58.** Erect axes with scar cells of trichoblasts on every segment. **59-61.** Upper portions of erect axes with branches arising in the axils of trichoblasts, 3-4 segments apart. Scale bars = 2 cm (Fig. 56), 80 µm (Fig. 57), 50 µm (Figs 58, 59), 500 µm (Fig. 60) and 200 µm (Fig. 61).



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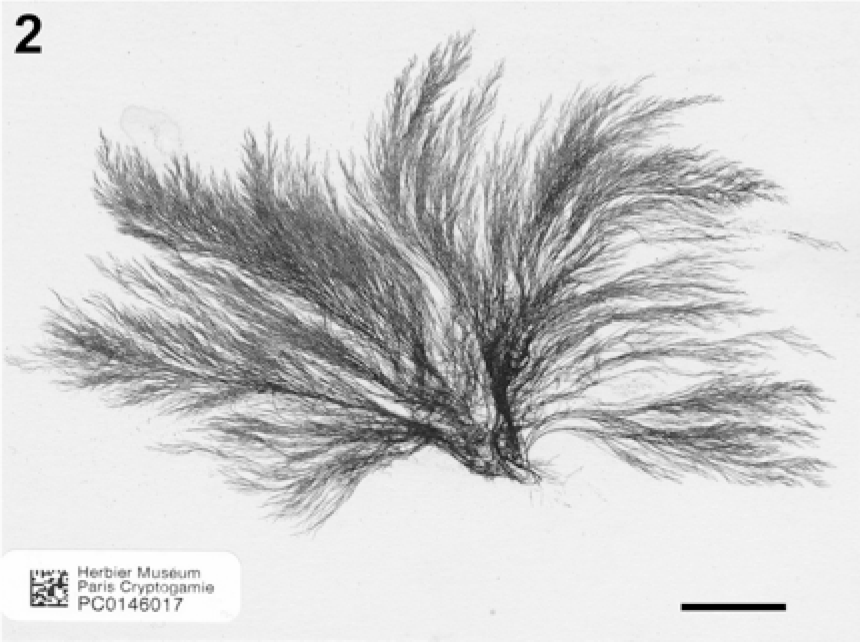

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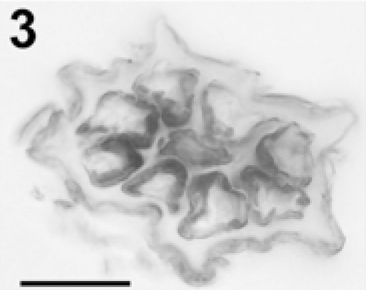

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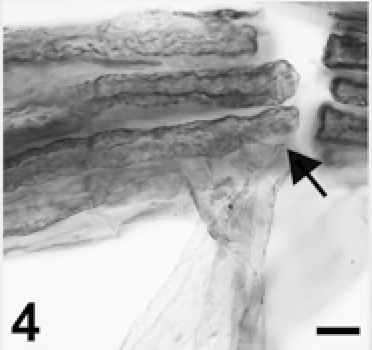

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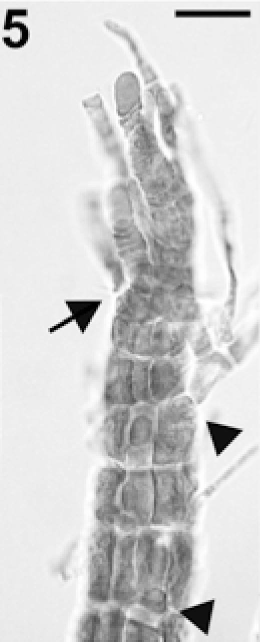

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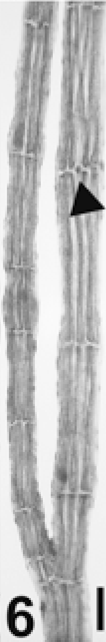

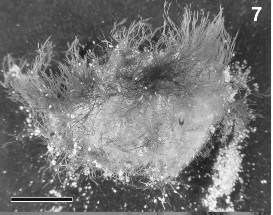
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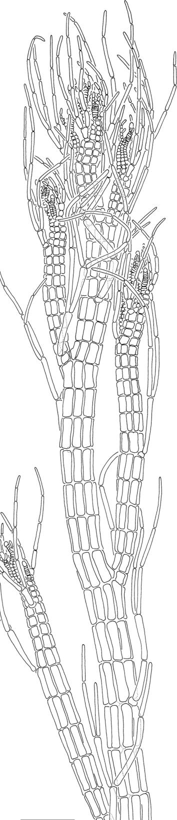
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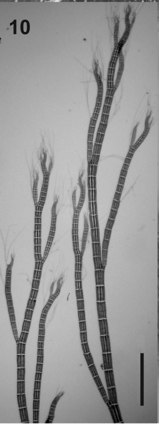
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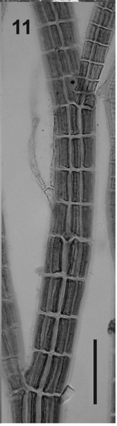
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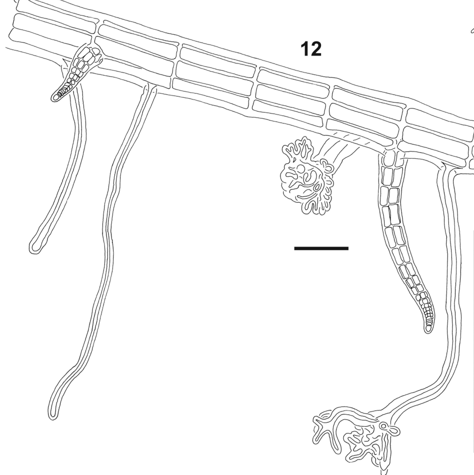
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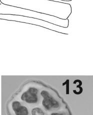
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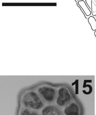
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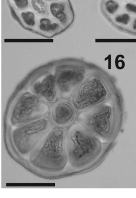
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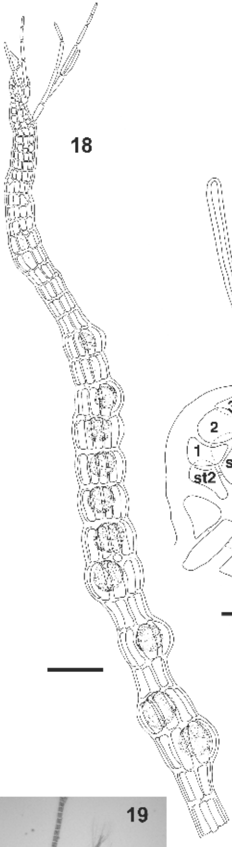

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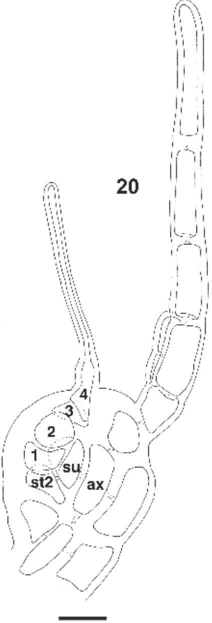

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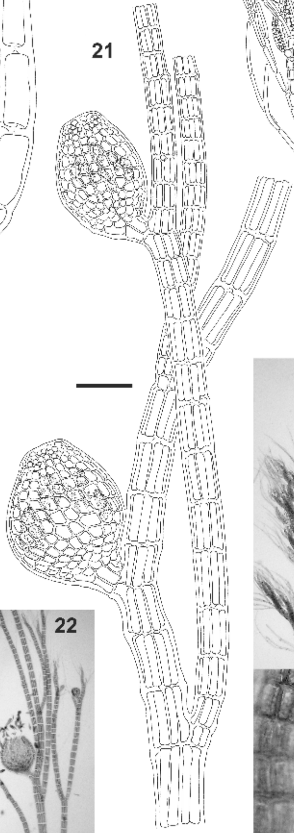

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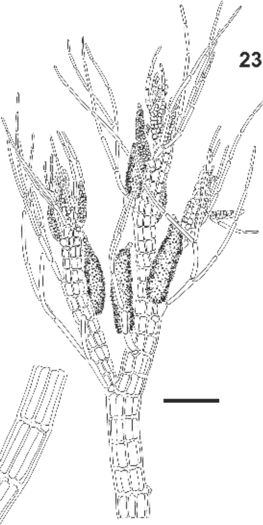

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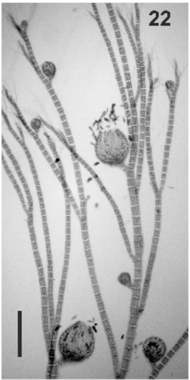

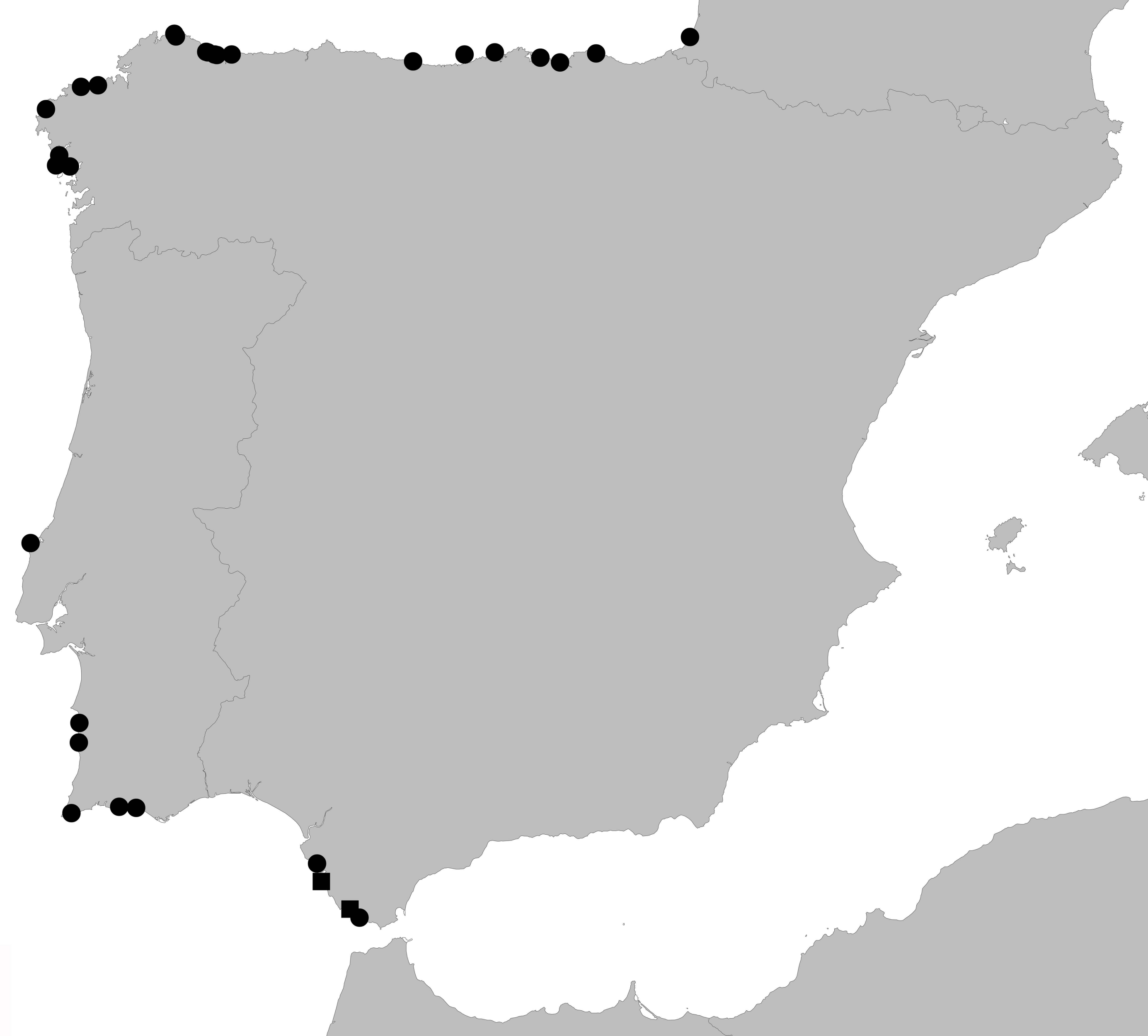

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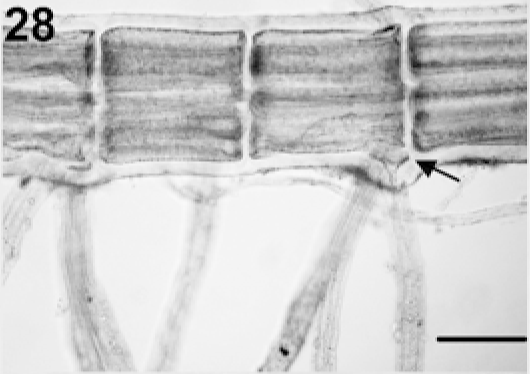

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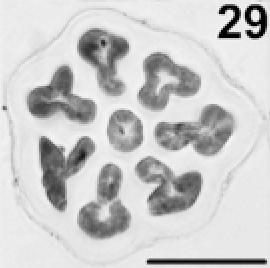

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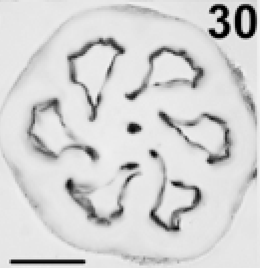

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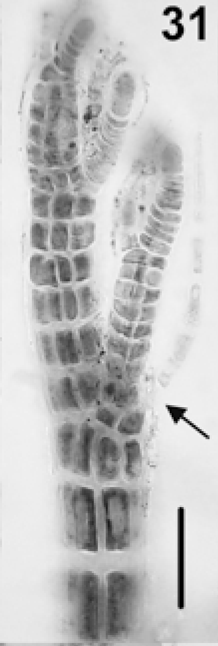

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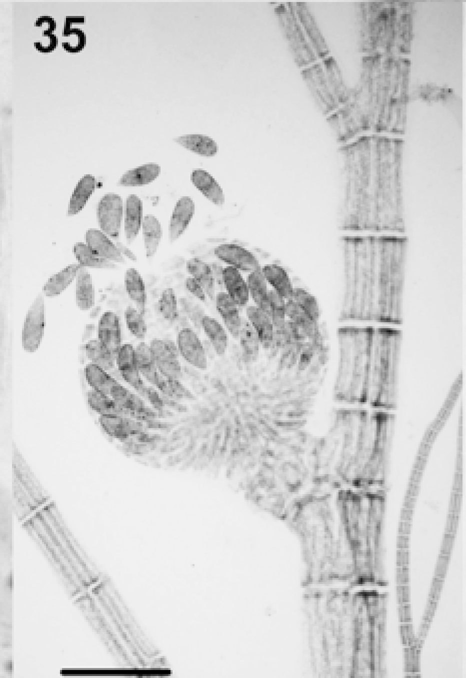

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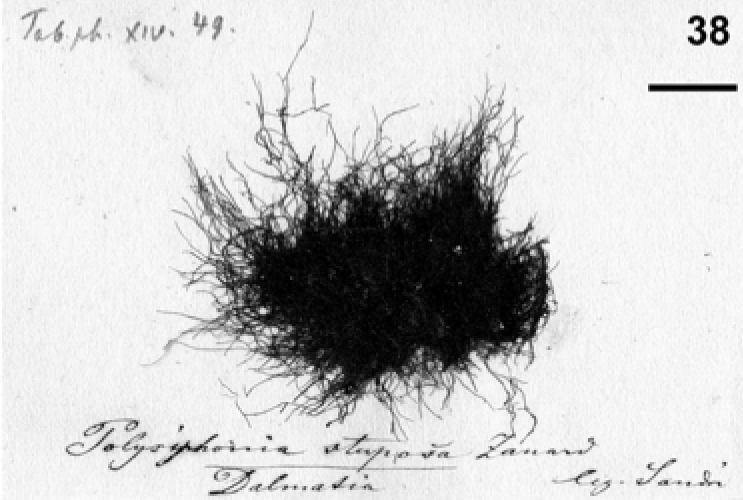
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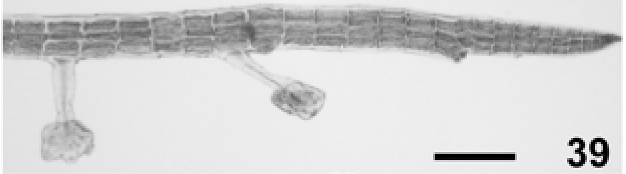

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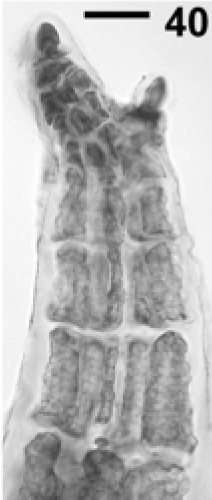

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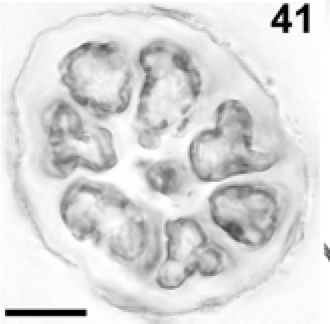

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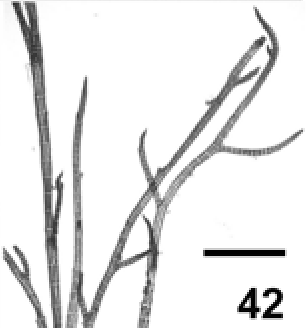

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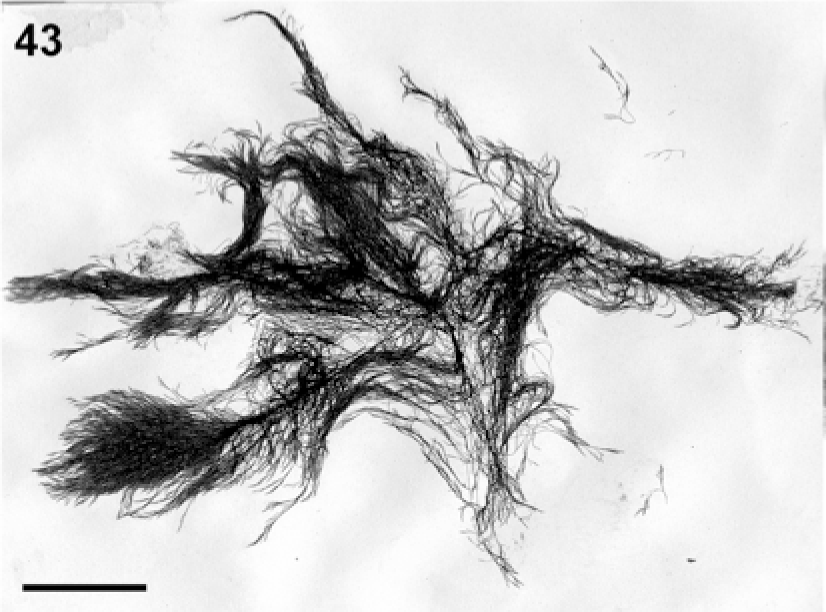
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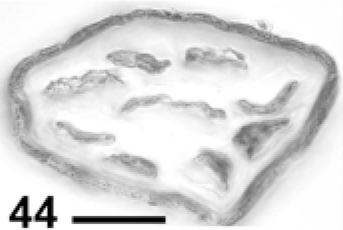
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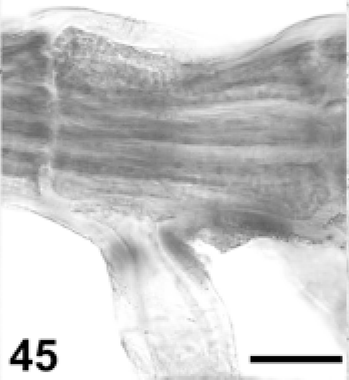
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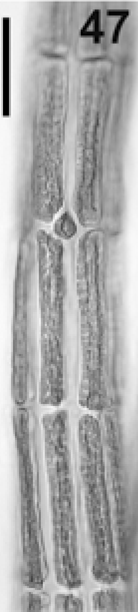
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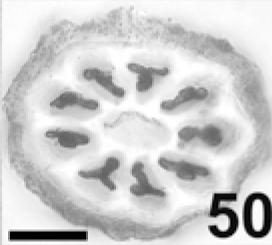

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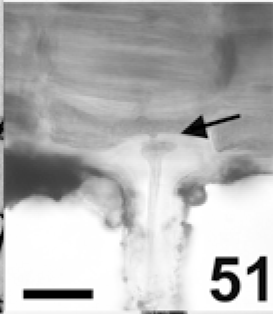

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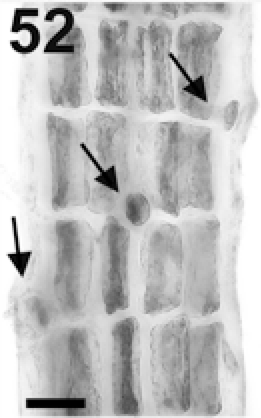

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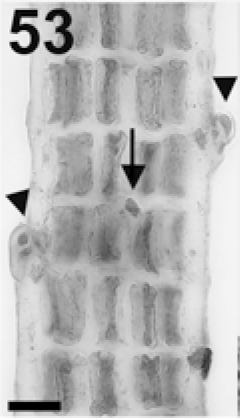

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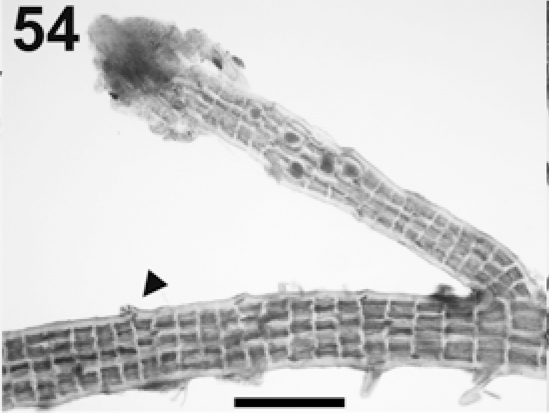

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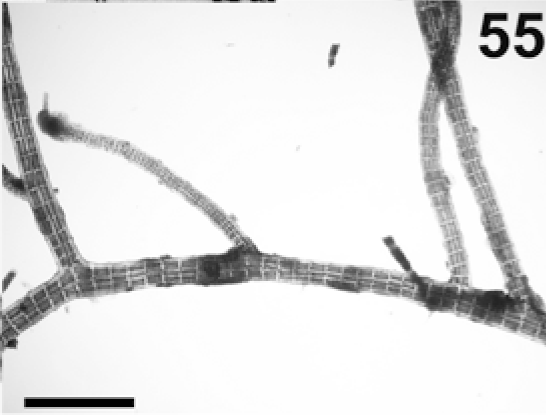

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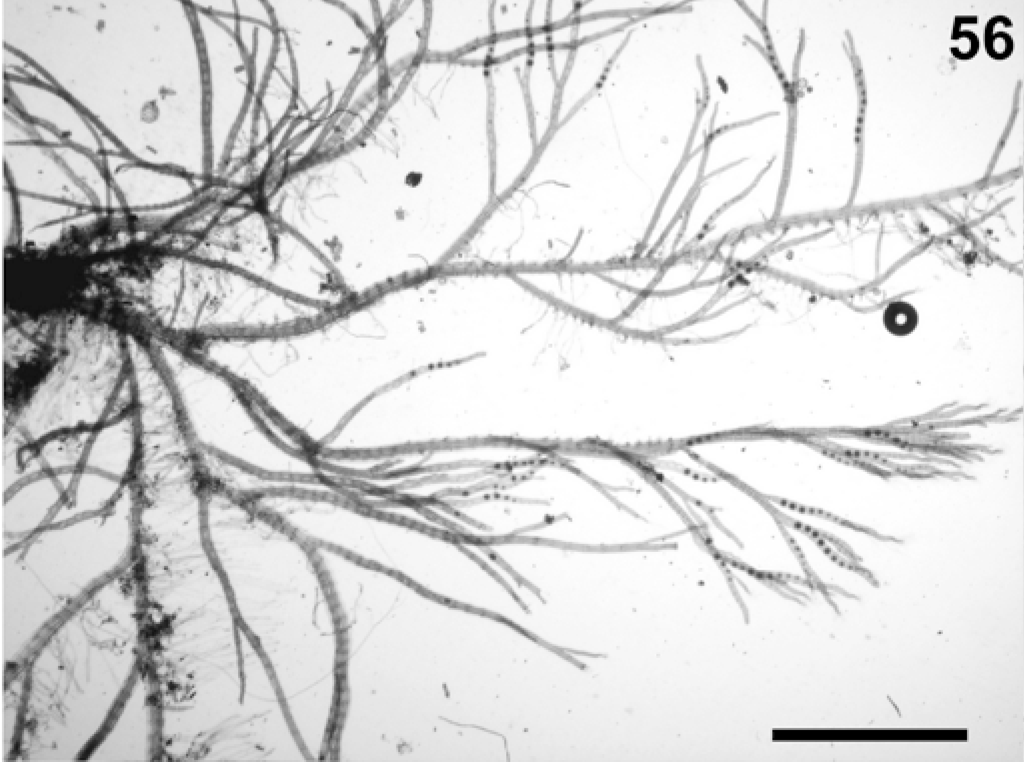

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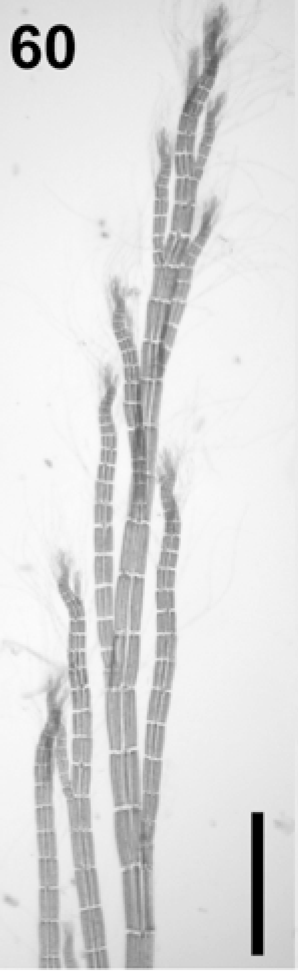

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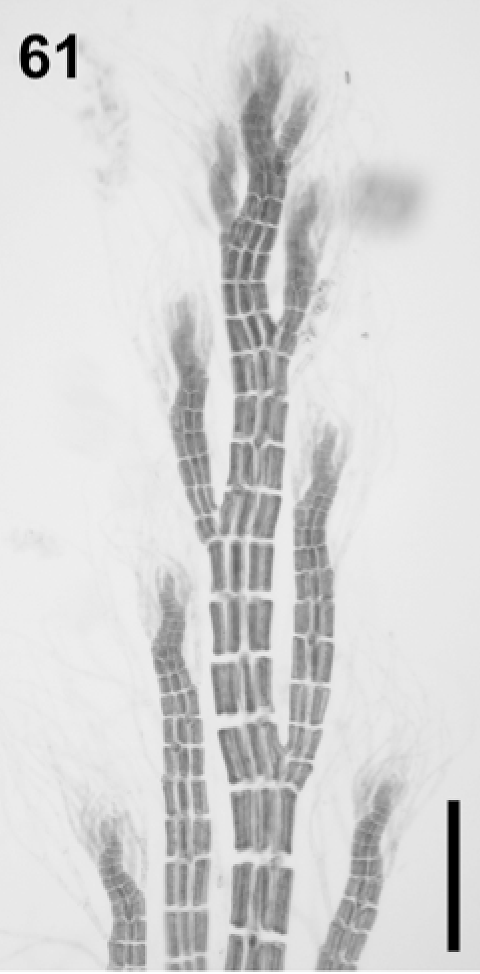


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Table S1. Materials collected during this study, including herbarium codes and Genbank accession numbers.

Species	Locality	Date	Collectors	Herbarium	GenBank
Polysiphonia brodiei creeping froms	Spain: Guipúzcoa, Igeldo (43º19’06’’N; 2º02’14’’W)	13.iii.2006	A. Secilla	BIO-4478	-
	Spain: Vizcaya, Elantxobe (43º23’59’’N; 2º37’54’’W)	7.x.2006	A. Secilla	BIO-4477	-
	Spain: Vizcaya, S. Juan Gaztelugatxe (43º26’41’’N; 2º46’41’’W)	15.iv.2007	A. Secilla	SANT-Algae 21651	JQ653296
	Spain: Asturias, La Franca (43º23’39’’N; 4º34'18"W)	23.iii.2011	I. Bárbara & P. Díaz	SANT-Algae 25600	-
	Spain: Lugo, San Ciprián (43º42’02’’N; 7º27’25’’W)	30.ix.2004	P. Díaz & I. Bárbara	SANT-Algae 26259	-
	Spain: A Coruña, Cambre (43º18’00’’N; 8º46’04’’W)	12.i.2009	P. Díaz & I. Bárbara	SANT-Algae 21623	JQ653297

	Spain: Cádiz, Cala Encendida (36º18’40’’N; 6º09’12’’W)	18.ii.2011	I. Bárbara & P. Díaz	SANT-Algae 26644	-
Polysiphonia brodiei erect forms	Spain: A Coruña, Sada (43º23’18’’N; 8º16’49’’W)	17.iv.2009	J. Cremades	SANT-Algae 22808	JQ653295
Polysiphonia elongata	Spain: Pontevedra, Tragove (42º31’35’’N; 8º49’39’’W)	30.iv.2010	J. Cremades	SANT-Algae 24097	JQ653299
Polysiphonia foetidissima	France: Biarritz (43º29’03’’ N; 1º33’46’’ W)	19.iii.2011	P. Díaz & I. Bárbara	SANT-Algae 25433	JQ653294
	Spain: Vizcaya, Laida (43º24’28’’N; 2º40’54’’W)	31.iii.2006	P. Díaz	SANT-Algae 20286	-
	Spain: Vizcaya, La Arena (43º21’16’’N; 3º06’53’’W)	07.ix.2006	P. Díaz	SANT-Algae 20971	-
	Spain, Vizcaya, La Arena (43º21’16’’N; 3º06’53’’W)	22.iii.2011	P. Díaz, I. Bárbara & A. Secilla	SANT-Algae 25638, 25657	-
	Spain, Vizcaya, La Arena	22.iii.2011	P. Díaz, I. Bárbara & A. Secilla	SANT-Algae 25644	JQ653290

(43º21’16’’N; 3º06’53’’W)				
Spain: Santander, Langre (43º28’37’’N; 3º41’37’’W)	06.xi.2010	P. Díaz	SANT-Algae 24620, 24628	-
Spain: Santander, Virgen del Mar (43º28’40’’N; 3º52’31’’W)	07.xi.2010	P. Díaz	SANT-Algae 24648	JQ653285
Spain: Asturias, La Franca (43º23’39’’N; 4º34'18"W)	23.iii.2011	I. Bárbara & P. Díaz	SANT-Algae 25611	JQ653291
Spain: Asturias, Niembro (43º26’33’’N, 4º50’20’’W)	08.x.2006	P. Díaz & C. Peteiro	SANT-Algae 21644	-
Spain: Asturias, Niembro (43º26’33’’N, 4º50’20’’W)	28.v.2010	P. Díaz & I. Bárbara	SANT-Algae 24162	-
Spain: Asturias, Sarello (43º33’27’’N; 6º58’39’’W)	28.vii.2010	P. Díaz	SANT-Algae 25166	-
Spain: Lugo, Catedrais (43º33’16’’N; 7º09’16’’W)	04.xi.2002	P. Díaz, I. Bárbara & T. Novo	SANT-Algae 16525	-

Spain: Lugo, Catedrais (43º33’16’’N; 7º09’16’’W)	20.ix.2005	P. Díaz	SANT-Algae 16577	-
Spain: Lugo, Catedrais (43º33’16’’N; 7º09’16’’W)	01.iii.2006	P. Díaz & V. Lagos	SANT-Algae 21622	JQ653292
Spain: Lugo, Catedrais (43º33’16’’N; 7º09’16’’W)	01.iii.2006	P. Díaz & V. Lagos	SANT-Algae 21650	-
Spain: Lugo, Catedrais (43º33’16’’N; 7º09’16’’W)	15.vii.2010	P. Díaz & I. Bárbara	SANT-Algae 24421	JQ653286
Spain: Lugo, Castro (43º33’47’’N; 7º10’35’’W)	24.iv.2009	P. Díaz & I. Bárbara	SANT-Algae 24656	-
Spain: Lugo, Llas (43º34’47’’N; 7º15’27’’W)	14.vii.2010	P. Díaz	SANT-Algae 24477	-
Spain: Lugo, Llas (43º34’47’’N; 7º15’27’’W)	19.iv.2011	P. Díaz, A. Secilla & V. Peña	SANT-Algae 27332	JQ653284
Spain: Lugo, Peinzás	15.vii.2010	P. Díaz & I. Bárbara	SANT-Algae 24412	JQ653289

(43º35’09’’N; 7º16’13’’W)				
Spain: Lugo, Peinzás (43º35’09’’N; 7º16’13’’W)	19.iv.2011	P. Díaz, A. Secilla & V. Peña	SANT-Algae 26245	-
Spain: Lugo, San Román (43º43’17’’N; 7º37’39’’W)	14.xi.2008	P. Díaz & I. Bárbara	SANT-Algae 21647	-
Spain: A Coruña: Xilloe (43º44’41’’N; 7º39’02’’W)	10.ix.2002	P. Díaz & I. Bárbara	SANT-Algae 24910	-
Spain: A Coruña, Barrañán (43º18’44’’N; 8º33’22’’W)	18.x.2002	P. Díaz & I. Bárbara	SANT-Algae 21645	-
Spain: A Coruña, Barrañán (43º18’44’’N; 8º33’22’’W)	16.vi.2003	P. Díaz & I. Bárbara	SANT-Algae 21646	-
Spain: A Coruña, Cambre (43º18’00’’N; 8º46'04"W)	14.iv.2008	P. Díaz & I. Bárbara	SANT-Algae 21648	-
Spain: A Coruña, Lago (43º05’53’’N; 9º11’50’’W)	29.ix.2003	P. Díaz & I. Bárbara	SANT-Algae 17963	-

Spain: A Coruña, Arnela (42º42’35’’N; 9º00’47’’W)	01.viii.2011	P. Díaz & V. García	SANT-Algae 26444	-
Spain: A Coruña, Basoñas (42º37’22’’N; 9º03’10’’W)	18.iv.2011	P. Díaz & I. Bárbara	SANT-Algae 26267	JQ653288
Spain: A Coruña, Basoñas (42º37’22’’N; 9º03’10’’W)	02.viii.2011	P. Díaz & V. García	SANT-Algae 26441	-
Spain: A Coruña, El Puntal (42º36’37’’N; 8º53’40’’W)	04.ii.2005	V. Peña & I. Bárbara	SANT-Algae 21649	-
Portugal: Estremadura, Baleal (39º22’25’’N, 9º19’56’’W)	14.vi.2010	P. Díaz & I. Bárbara	SANT-Algae 24255	JQ653287
Portugal: Baixo Alentejo, Queimado (37º49’34’’N; 8º47’34’’W)	24.iv.2005	P. Díaz	SANT-Algae 24658	-
Portugal: Baixo Alentejo, Almograve (37º39’54’’N; 8º48’04’’W)	25.v.2005	P. Díaz	SANT-Algae 24657	-
Portugal: Algarve, Ingrina	09.v.2005	P. Díaz	SANT-Algae 24659	-

	(37º02’46’’N; 8º52’43’’W)				
	Portugal: Algarve, Ingrina				JQ653293
	(37º02’46’’N; 8º52’43’’W)	20.ii.2011	P. Díaz & I. Bárbara	SANT-Algae 25470	
	Portugal: Algarve, Armaçao de Pera				-
	(37º06’04’’N; 8º22’17’’W)	17.x.2005	P. Díaz	SANT-Algae 24840	
	Portugal: Algarve, Olhos d'Agua				JQ653283
	(37º05’20’’N; 8º11’27’’W)	20.ii.2011	P. Díaz & I. Bárbara	SANT-Algae 26464	
	Spain: Cádiz, Puerto de Santa María				-
	(36º34’48’’N; 6º15’51’’W)	16.xi.2005	P. Díaz	SANT-Algae 26069	
	Spain: Cádiz, Punta Plata				-
	(36º06’28’’N; 5º49’41’’W)	19.i.2011	P. Díaz & I. Bárbara	SANT-Algae 26517	
Polysiphonia schneideri	Spain: Cádiz, Santa Leocadia				-
	(36º25’15’’ N, 6º13’02’’ W)	9.vi.2010	M. Fernández-Lora	SANT-Algae 26813	
	Spain: Cádiz, Santa Leocadia				JQ653298
	(36º25’15’’ N, 6º13’02’’ W)	23.ii.2011	M. Fernández-Lora	SANT-Algae 26065	

Spain: Cádiz, Barbate (36º11’03’’ N, 5º55’39’’ W)	18.ii.2011	P. Díaz & I. Bárbara	SANT-Algae 26572	-